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Decomposition and nutrient dynamics of leaf litter in litter bags of two mesh sizes set in two dipterocarp forest sites in Peninsular Malaysia

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Summary. Carbon and nutrient dynamics patterns of *Dipterocarpus baudii* leaf litter in a plantation forest and of mixed leaf litter in a lowland dipterocarp forest were investigated using litter bags with two mesh sizes (0.5 mm and 2.0 mm) which allow differential access of soil fauna. The decomposition rate constants (Olson's k) were significantly higher in the coarse mesh bags (k= 1.64 and 2.15 in the plantation and dipterocarp forest sites, respectively) than in the fine mesh bags (k = 1.02 and 0.76 in the plantation and dipterocarp forest sites respectively), suggesting that soil animals especially termites accelerated the leaf litter decomposition by their feeding. Further, the nutrient dynamics of decomposing leaf litter differed between the coarse and fine mesh bags. Nutrient mass released was higher in the coarse than in the fine mesh litter bags, suggesting that termites feeding activities enhanced nutrient mobilization in both study sites.

Key words: Carbon and nutrient dynamics, carbon to nitrogen ratio, immobilization, mobilization , termites, tropical forests

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Introduction

Decomposition rates and nutrient dynamics of leaf litter are influenced by the composition of decomposer communities in the soil systems (Swift et al. 1979). Litter bags with different mesh sizes have been used to manipulate the composition of these communities (Crossley & Hoglund 1962). In forest sites with minimum faunal influence, microbial populations mainly contribute to immobilization and mobilization of nutrients (Berg & Staaf 1981; Berg 1986). In the mull sites of temperate forests, macro-soil animals significantly contribute to the weight loss and nutrient mobilization by their feeding activities (Joergensen 1991; Petersen & Luxton 1982).

In the tropical forests, termites are an important faunal component for litter decomposition (Abe & Matsumoto 1979; Petersen & Luxton 1982). In Malaysian tropical forests, the consumption of leaf litter by macrotermes termites, such as *M. malaccensis* and *M. carbonarius*, account for about 20 to 30% of annual litter fall (Matsumoto & Abe 1979). Termites contribute to the disappearance of leaf litter by their feeding activities in tropical forests, but there

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rather are few studies on the role of termites on the nutrient dynamics in tropical forests with a mull humus form.

The purpose of this study is to demonstrate the roles of soil animals, especially termites, on the decomposition processes of *Dipterocarpus baudii* leaf litter in a plantation forest and of mixed leaf litter in a lowland dipterocarp forest. In this paper, decomposition rates and nutrient dynamics of the leaf litter were studied by the litter bag method at the study sites. Then, the roles of soil animals on the carbon and nutrient dynamics were evaluated by a comparison between the defaunated and control litter bags.

Materials and Methods

Site description

This study was carried out in a plantation of *Dipterocarpus baudii* Korth (Dipterocarpaceae) and a lowland dipterocarp forest. The plantation of *D. baudii* was established at the campus of Forest Research Institute Malaysia (FRIM), which located at Kepong (3° 14′N and 101° 38′E) near Kuala Lumpur, Peninsular Malaysia. Details of the *D. baudii* plantation site are given in Yamashita et al. (1995). Another study site was chosen in a lowland dipterocarp forest in Pasoh Forest Reserve, about 140 km southeast of Kuala Lumpur (2° 58′N and 102° 18′E).

Soils of the plantation are described in Yamashita et al. (1995) and the soil of Pasoh Forest Reserve is granite-derived, belonging to the Tampin series (Allbrook 1973). In both study sites, soil humus was of the mull type and consisted mainly of litter (L). Amounts of soil organic layer (A_0) comprised 4.3 and 4.9 tonnes per ha in the Pasoh and FRIM sites, respectively. In both study sites, dominant decomposers of leaf litter are termites (Chiba 1978; Abe & Matsumoto 1979; Tho 1992). Termites are a representative group of macro-soil fauna in the Pasoh forest (Abe & Matsumoto 1979). The list of termites of the FRIM site are listed in Table 1. Annual precipitation was 2220 mm in FRIM and 1832 mm in Pasoh during a 12 month-period from June 1992 to May 1993. Mean temperature was 27.6 °C (FRIM) and 25.7 °C (Pasoh forest), respectively.

Table. 1. A list of termite species collected in the *D. baudii* plantation in the FRIM site. *Macrotermes malaccensis* (Haviland) was a dominant species in this site.

Family	Species
Termitinae	*Microcerotermes serrula* (Desneux) *Pericapritermes sp. B* (as in Tho 1992)
Macrotermitinae	*Macrotermes malaccensis* (Haviland) *Odontotermes sp.1.* (as in Tho 1992)
Nasutitermitinae	*Bulbitermes singaporensis* (Haviland) *Bulbitermes perpusillus* (John)

Litter bag experiment

Amounts of fine litterfall ranged from 9.3 to 12.8 tonnes ha^{-1} yr^{-1} (1991–1993) in the plantation (Yamashita et al. 1995) and was 8.6 tonnes ha^{-1} yr^{-1} (1991–1992) in Pasoh. Leaf litter fall was 5.5 to 8.1 tonnes ha^{-1} yr^{-1} in the *D. baudii* plantation and 6.2 tonnes ha^{-1} yr^{-1} in a lowland dipterocarp forest, respectively.

The leaves collected during litterfall measurement were used in the *D. baudii* plantation experiments. Collected leaf litter was brought back to the laboratory of FRIM and air-dried at 40 °C for 48 h in a drying oven. Air-dried samples were sorted and then newly fallen leaves were selected for the litter bag samples. In the Pasoh forest, newly fallen leaf litter of *Shorea lepurosula* Miq. (Dipterocarpaceae) and *Heritiera javanica* (Bl.) Kosterm (Sterculiaceae) was collected from the forest floor and used for the litter bag study.

In both studies, two types of litter bags were used: a) fine litter bags (0.5 mm stainless steel mesh) to exclude meso- and macro-animals, and b) coarse litter bags (2.00 mm nylon mesh) allowing entry of all decomposer groups. In fact, some coarse litter bags were torn by animals during field incubation. The size of each litter bag was 20 cm × 20 cm. Each litter bag contained 10.0 g of air-dried leaf litter. In the FRIM site, leaf litter of *D. baudii* was used for the decomposition study, while at Pasoh sites, mixed leaf litter of 5.0 g of *Shorea lepurosula* and 5.0 g of *Heritiera. javanica* was enclosed into each bag .
Sixty litter bags with mesh size of 2 mm and thirty litter bags of 0.5 mm were laid out within the plantation sites (20 m × 30 m) in September 1992. Ten coarse litter bags were collected on six sampling occasions at monthly intervals, and ten bags of fine litter bags were collected at bimonthly intervals in the plantation. At the Pasoh site, fifty litter bags of each type were set on the forest floor in the study site (20 m × 20 m). Ten bags of each type were collected at monthly intervals during the study period. Litter bags were immediately air-dried at 40 °C for 48 h in a drying oven. After brushing soil particles and other dust off the leaf surface, we measured the weight of air-dried samples by an electric balance.

Chemical analysis

Chemical analysis of leaf litter was carried out for the samples of *D. baudii* incubated in the FRIM plantation. Contents of organic and mineral constituents were analyzed in the Laboratory of Forest Ecology, Kyoto University. Air-dried samples were ground with a laboratory mill to pass a 0.5 mm screen. After preparation, total carbon (C) and total nitrogen (N) were analyzed by an automatic gas chromatograph (CN corder, type MT-600, Yanaco Co. Kyoto, Japan). In preparation for nutrient analysis, ground samples were digested in nitric acid and perchloric acid. Phosphorus (P), potassium (K), sodium (Na), magnesium (Mg), calcium (Ca), manganese (Mn), aluminium (Al), and ferrous ion (Fe) were analyzed with an Inductively Coupled Plasma Atomic Emission Spectrometer (type SPS 1500 VR, SEIKO Instrumental Inc. Tokyo, Japan). Initial contents of lignin and cellulose, and polyphenols were quantified by the method of Goering & van Soest (1970) and Quamby & Allen (1989), respectively.

Results

Disappearance of leaf litter

Fig. 1 shows the weight loss of *D. baudii* leaf litter and mixed leaf litter in two types of litter bags during the study period. In the FRIM site, litter in coarse bags and fine bags lost 62 % and 38 %, respectively, of their initial weights during a six-month incubation. In Pasoh, leaf litter in coarse and fine bags lost 53 % and 27 % of their initial weight during the 5 month field incubation. The decomposition rate of leaf litter was estimated using the single exponential decay model of Olson (1963),

$$DM \times 100 / DM_0\ [\%] = 100 \times \exp(-k\ t)$$

where k is the decay constant, t is the year, DM_0 is the original mass of dry matter and DM is the mass of dry matter after a given period.
Decomposition rates in coarse and fine bags were 1.64 and 1.02, respectively, in the plantation and were 2.15 and 0.76 in Pasoh (Table 2). In both study sites, decomposition rates of leaf litter were significantly higher in the coarse than in the fine litter bags ($P < 0.01$).

Table 2. Decomposition rate constant (k $year^{-1}$) of *D. baudii* and mixed leaf litter in the coarse and fine litter bags.

Species	(k $year^{-1}$)	study site
Dipterocarpus baudii leaf litter	1.64 in coarse mesh	*D. baudii* plantation
	1.02 in fine mesh	*D. baudii* plantation
Mixed litter of *Shorea lepurosula* and	2.15 in coarse mesh	Pasoh forest site
Heritiera javanica	0.76 in fine mesh	Pasoh forest site

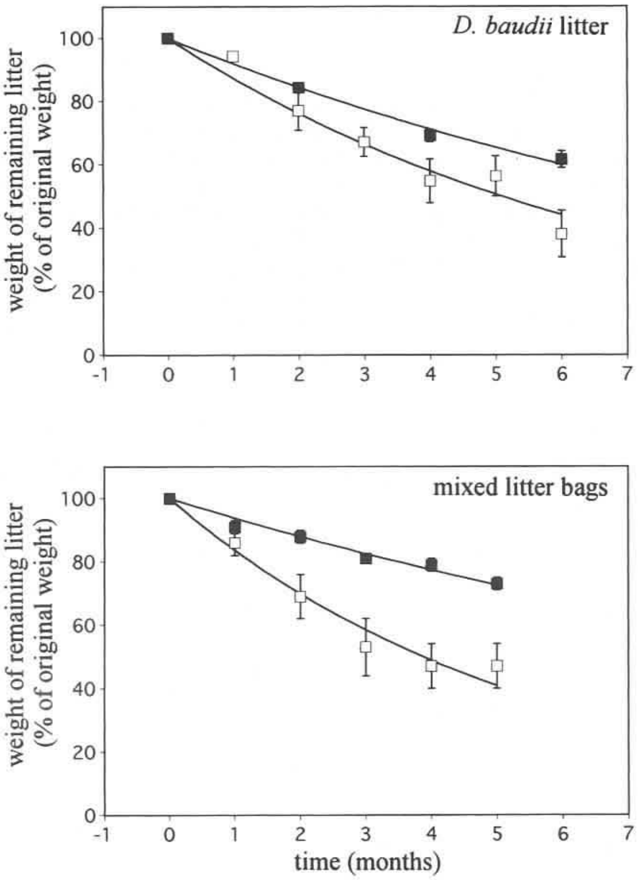

Fig. 1. Changes in weight remaining in the coarse (□) and in the fine (■) litter bags during the decomposition period. Bars show the standard errors. Mixed litter bag contained leaf litter of two tree species, *Shorea lepurosula* and *Heritiera javanica*

The variability of mass loss among the individual litter bags represents another aspect of decomposition processes. The variability of mass loss was expressed by the coefficient of variation (CV). The changes in variability are shown in Table 3. Variability of mass loss in both litter bags increased with the advance of decomposition in the two study sites. On all sampling occasions, variability of mass loss was higher in the coarse bags than in the fine litter bags.

Table 3. Changes in variablity of mass loss among the individual litter bags (n = 10). The variability of mass loss is experessed by CV; CV= (standard deviation/ mean) × 100 (%)

Month	*1*	*2*	*3*	*4*	*5*	*6*
D. baudii (coarse litter bags)	5.2	24.0	20.7	37.8	34.1	58.3
D. baudii (fine litter bags)	–	3.2	–	8.2	–	13.3
Mixed leaf (coarse litter bags)	13.6	30.4	49.3	42.5	42.0	–
Mixed leaf (fine litter bags)	7.0	6.4	4.1	6.2	6.7	–

Chemical changes

Table 4 shows litter qualities of *D. baudii* leaves. Nutrient concentrations of decomposing leaf litter changed with incubation time (Fig. 2). Changes in nutrient concentrations showed a similar pattern between the fine and coarse litter bags, and were classified into three groups. The first group consisting of N, Ca and Mn, showed small leaching loss and immobilization. The leaching loss occurred during the first 2 months and was higher in the coarse than in the fine litter bags. The second group consisted of Fe and Al and showed significant net immobilization throughout the study period. Concentrations of Al and Fe were increased ten to fifty times. The third group consisted of P, K, and Mg. The concentrations of these nutrients decreased by leaching loss during the first two months and then maintained a low level throughout the experiment. The pattern of Na changes belongs to none of the 3 groups. The leaching losses of N, Ca, Mn, P, K, and Mg occurred during the first 2 months and were higher in the coarse than in the fine litter bags.

Table 4. Leaf litter quality of *Dipterocarpus baudii* and are expressed by the contents of macro nutrients (N, P, K, Na, Mg and Ca) and micro nutrients (Mn, Al, Fe) and organic components (lignin, cellulose, polyphenols and total carbon)

Litter quality	*Components*					
Carbon components	Lignin	Cellulose	Polyphenols	Total carbon		
% of dry mass	42.2	24.5	1.59	48.2		
Macro–nutrients	N	P	K	Na	Mg	Ca
% of dry mass	1.23	0.050	0.222	0.012	0.125	0.709
Micro–nutrients	Mn	Al	Fe			
% of dry mass	0.024	0.013	0.023			

The changes in nutrient mass, together with those of organic mass, are shown in Fig. 3. Changes in nutrient mass are also classified into three groups. The amounts of Fe and Al increased with organic matter loss. Amounts of remaining N, Ca, Mn, P, and, Mg mass were significantly higher in fine litter than in the coarse litter bags at the end of experiment ($p<0.01$). K and Na showed no clear difference ($p>0.10$) between the two types of litter bags. Mass loss of nutrients was higher in the coarse litter than in the fine litter bags during the study period. The results are reflected in the larger amount of organic matter remaining with higher nutrient concentrations in the fine litter bags.

Changes in C/N ratios during decomposition

Nitrogen dynamics followed the leaching (one month), immobilization (2–3 month) and mobilization (3–4 month) phases during decomposition, while the carbon was mobilized throughout the 6 month period. The C/N changes during the decomposition resulted from the nitrogen and carbon dynamics. Fig. 4 shows the changes in C/N ratios of individual litter bags during the decomposition in the plantation site. From initial to the 1–2 month samples, C/N ratio increased in both fine and coarse litter bags through the leaching loss of nitrogen. Then, C/N ratio decreased with the immobilization of nitrogen and the mobilization of carbon during decomposition. Then, C/N ratio attained a critical value of about 38 and 34 in the fine and coarse litter bags, respectively. The critical value of C/N was significantly higher in the fine litter bags than in the coarse litter bags($P<0.01$). Thus, the immobilization of nitrogen is higher in the fine than in the coarse mesh bags (Fig. 2 and 3).

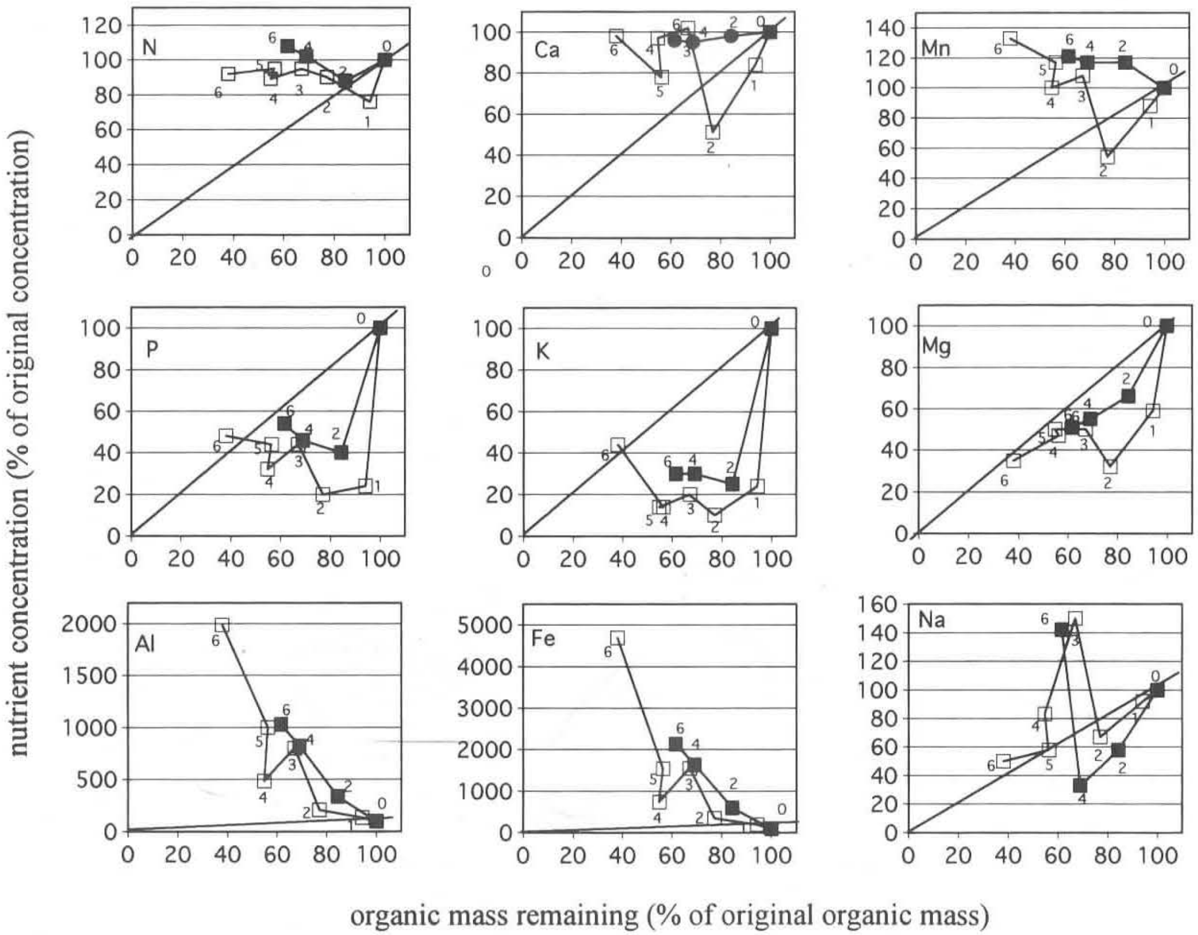

Fig. 2. Relationships between the percent litter mass remaining and the percent nutrient concentration of original concentration. Number (1 to 6) shows the field incubation period (in months)

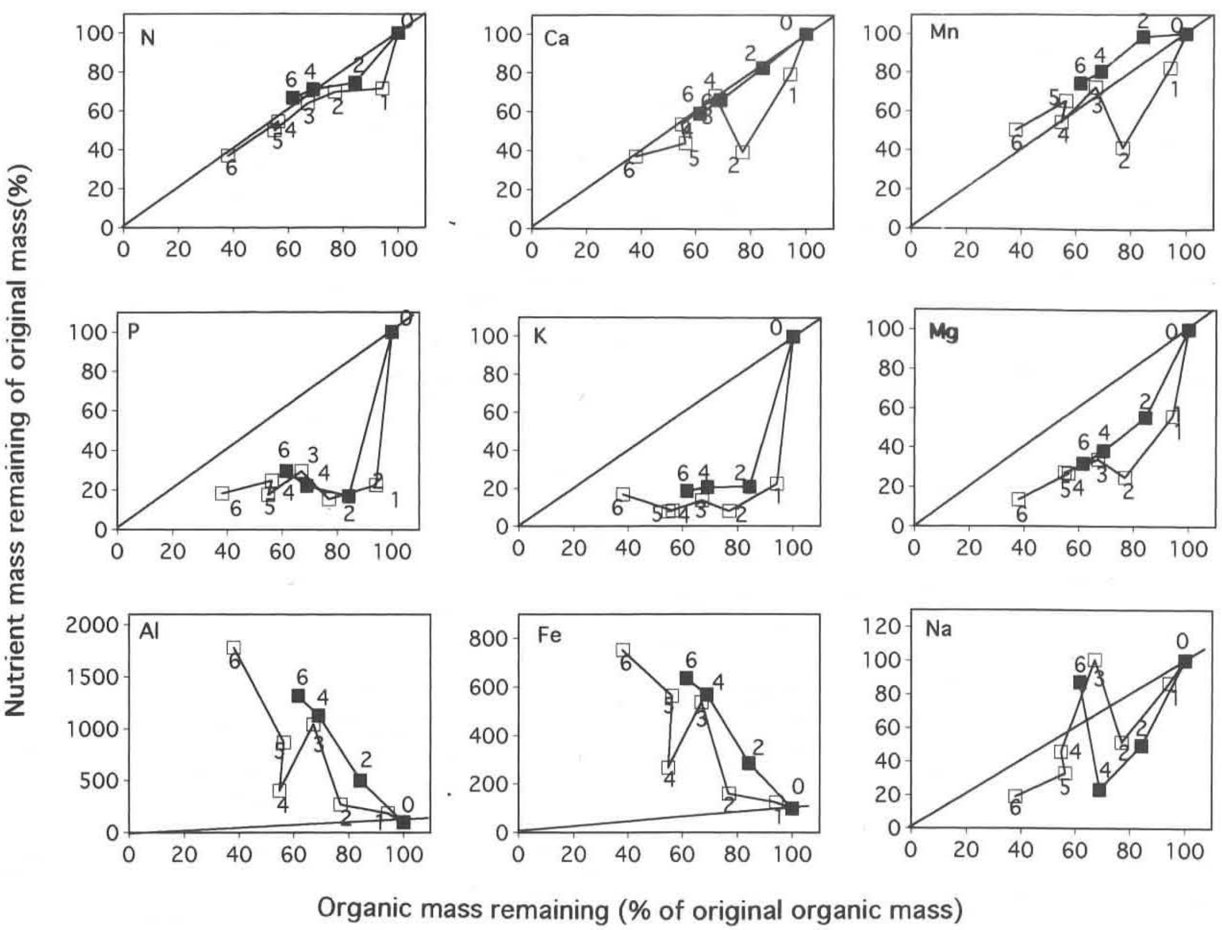

Fig. 3. Relationships between the perecent organic mass remaining (%) and the percent nutrient mass remaining of original mass (%) at the 1, 2, 3, 4, 5 and 6 month incubation

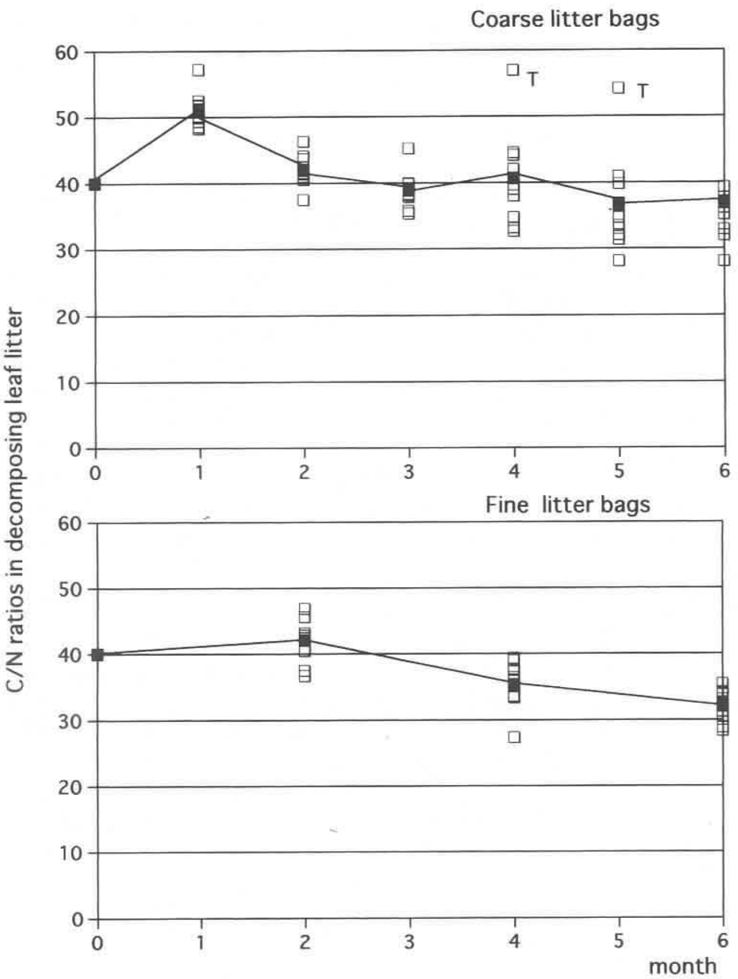

Fig. 4. Changes in C/N ratios during the decomposition of leaf litter. The C/N ratio of individual litter bags are shown for each incubation period from 0 to 6 months. In the figure for coarse litter bags, T indicates the C/N values for the litter remaining (petiole and midvein) in the bags after the feeding by termite

Discussion

Weight loss of leaf litter

Decomposition rates are rapid in tropical forests characterized by high, constant temperature and high annual rainfall (Olson 1963). Takeda (1996) summarized the decomposition rates of leaf litter in both temperate and tropical forests. The mean decomposition rates are $k = 1.85$ and 0.93 in tropical and temperate forests, respectively. In the present litter bag experiments, decomposition rates of leaf litter were significantly higher in the coarse (2 mm mesh) bags than in the fine (0.5 mm mesh) bags in both study sites. In the coarse bags, decomposition rates of leaf litter were comparable with those in tropical forests (Takeda 1996), while the decomposition rates of the fine litter bags were rather more comparable with those in temperate forests.

There are few comparative studies for the present experiments. Comparisons of decomposition rates between fine and coarse mesh was studied for scrub leaf litter in Nigerian bush-fallow (Swift et al. 1981), tree leaf litter in Gunung Mulu, Sarawak (Anderson et al. 1983), maize and wheat roots in India (Singh & Shekhar 1989) and prunings of woody agroforestry plants (Tian et al. 1992). Most of these case studies demonstrated the significant contribution of soil macrofauna on decomposition processes with the exception of Mulu, Sarawak (Anderson et al. 1983). Thus, the litter bag experiments showed a significant contribution of soil macro-fauna to the decomposition by leaf litter in tropical forests.

Termites are a representative group of macro-soil fauna in the Pasoh forest (Abe & Matsumoto 1979). In the plantation of FRIM, termites were also important decomposers. Six species of termites are present in or near the plantation including four leaf feeder species (e.g. *M. malaccensis*) (Abe 1979). Feeding traces of termites are easily identified in the litter samples. According to our field observations on decomposing leaf litters, some samples of leaf litters in the 2 mm bags were attacked all parts, except the petioles, by termites. This led to reduction in surface area of leaf litter attacked. The litter samples attacked by other decomposer agents kept their original leaf shapes. *M. carbonarius* is abundant in Pasoh and rare in FRIM, and this species prefers newly fallen litter. In FRIM, *M. malaccensis* is the dominant species and prefers older leaf litter. In this study, the feeding of soil macrofauna including termites, accounted for about 24 % per 6 months (FRIM site), and 27 % per 5 months (Pasoh site) of leaf litter weight loss. Abe and Matsumoto (1979) estimated the rates of consumption by termites in the litter layer in the Pasoh forest as were 30–35 % per 6 months which comparable with the present study.

The variations of decomposition rates between litter bags were evaluated by CV values. Values of CV were higher in coarse than in fine bags in both study sites. Soil fauna ingested leaf materials from the early stage of decomposition in Pasoh and did so gradually in the FRIM plantation. We laid litter bags randomly on the forest floor. Termites attacked the samples located on the places where they can reach. The foraging behaviour of termites may cause a high variability in decomposition rates of coarse litter bags. So termites contributed significantly to the weight loss of leaf litter in both study sites. Further, termite feeding activities not only accelerated the decomposition rates, but also contributed to the variability of decomposition rates of litter bags set in the forest floor in both study sites.

Nutrient dynamics of leaf litter

Generally, nutrient dynamics of leaf litter consists of the three phases; leaching, immobilization and mobilization. Al and Fe showed only immobilization phases throughout the decomposition processes. During this phase, net accumulation in decomposing leaves suggested the immobilization of Al and Fe from mineral soil to the litter bags. The immobilization processes of Al and Fe were not very different between the two types of litter bags. Second group: N, Ca, Mn, and Mg followed the leaching, immobilization and mobilization phases. In these elements, the leaching loss was significantly higher in the coarse than in the fine mesh bags. Third group: P and K showed leaching and immobilization phase during decomposition. The leaching intensities was higher in the coarse than in the fine mesh. The immobilization processes of these nutrients were not influenced by mesh size.

The differences in leaching loss between litter bag types were apparent for all nutrients and may be explained by 1) physical factors such as impacts of raindrops affecting the leaching loss of nutrients such as Mg, Mn and Ca losses from the leaf litter of the 2 mm bag, 2) immobilization of nutrients by microbial populations. During the first 2 months, feeding of termites could not account for the differences in weight loss between the two bag types. So, the initial leaching loss may reflect physical factor, such as the effect of rain drops rather than the biotic effects, such as immobilization by microbial populations.

The difference in critical nitrogen level between the coarse and the fine litter bags may be explained by the feeding of soil animals on the N-rich parts of decomposing litter. The critical values of the C/N ratio were 38 and 34 in the coarse and fine litter bags, respectively. The

lower critical value of fine litter bags suggests the immobilization of N by the microbial populations (Swift et al. 1981; Tian et al. 1992; Constantinides & Fowens 1994). So, the feeding of soil animals contributed to the nitrogen mineralization of leaf litter. The C/N ratio at critical nitrogen level is reported to be 20–30 in temperate and boreal forest (Berg & Staaf 1981) and may be higher in tropical forests.

Litter consumption by termites caused changes in nutrient dynamics directly and indirectly. The direct effect on nutrient dynamics is removal of organic matter containing nutrients from litter bags through feeding activities. The direct effects on nutrient dynamics are apparent for the six elements, N, C, Mn, P, K, and Mg at the end of the 6 month experiment in this study. The amount of remaining Al and Fe was higher in the course litter bags possibly because of the transfer of soil materials by termites. The soil materials that was transferred by termites increased the Fe and Al contents. The feeding preferences of termites also have an indirect effect on nutrient dynamics. The termites prefer the nutrient-rich parts of leaf litter, such as leaf blades (Takeda et al. 1984). The present litter bag experiment demonstrates that the termites are effective in reducing microbial nutrient immobilization by preferential feeding on nutrient-rich parts of leaf litter. Thus, feeding of termites reduced the immobilization processes of Mn, Mg, K, and N by microbial populations. These indirect effects have been observed in the decomposition processes of leaf litter in tropical forests (Swift et al. 1981; Tian et al. 1992).

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